Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Regularia

I.D. Lindley

Department of Geology, Australian National University, Canberra, A.C.T. 0200

Lindley, I.D. (2003). Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Regularia. *Proceedings of the Linnean Society of New South Wales* **124**, 137-151.

Regular sea urchins are an important component of the rich and diverse echinoid fauna of the Lower Pliocene Kairuku Formation, Yule Island, Papua New Guinea. Seven taxa are recognised, including the cidaroids *Phyllacanthus imperialis* var. *javana* K. Martin, 1885, *Phyllacanthus* sp. and *Prionocidaris verticillata* (Lamarck, 1816), the toxopneustids *Cyrtechinus verruculatus* (Lütken) and *Schizechinus* cf. *tuberculatus* (Pomel), a temnopleurid *Temnotrema macleayana* (Tenison-Woods) and a parasaleniid *Parasalenia poehli* Pfeffer, 1887. The cidaroids, parasaleniid and temnopleurid occupied shallow-water reef habitats. The toxopneustids were dominant herbivores in adjacent seagrass meadows. The strong affinities evident between the seagrass meadow- and shallow-water sand-dwelling echinoid faunas of Yule Island and fossil and extant faunas of the Red Sea region, parallel the geographic patterns of species diversity of Indo-Pacific seagrasses, corals and mangroves.

Manuscript received 30 September 2002, accepted for publication 19 November 2002.

KEYWORDS: *Cyrtechinus*, Echinoidea, Palaeoecology, Papua New Guinea, *Parasalenia*, *Phyllacanthus*, Pliocene, *Prionocidaris*, Regularia, *Schizechinus*, *Temnotrema*

INTRODUCTION

The Tertiary faunas of Yule Island, and along the south coast of eastern New Guinea (Montgomery 1930), represent the nearest marine fossil occurrences to the Great Barrier Reef (Fig. 1). The Great Barrier Reef's rich and diverse shallow-water echinoderm fauna, in particular, has been intensively documented, including (from north to south) the Murray Islands in Torres Strait (H.L. Clark 1921), Cairns-Pipon Island-Raine Island region (Gibbs et al. 1976), Low Isles (H.L. Clark 1932; Endean 1956), Swain Reefs (A.M. Clark 1975) and the Capricorn-Bunker Groups (Endean 1953). Although it is widely accepted that a significant component of the echinoderm faunas of tropical Australia migrated southward from the East Indies via the Torres Strait or the Arafura Sea (A.H. Clark 1911; H.L. Clark 1946; Endean 1957), with no marine Tertiary record in Queensland, palaeontology has not been of use in determining migrations to this region (Endean 1957). Torres Strait prior to the late Quaternary was emergent (Australasian Petroleum Company 1961; Struckmeyer et al. 1993) and the eastern coast of New Guinea was in closest faunistic contact with the Great Barrier Reef, the coastline at the time (H.L. Clark 1946; Ekman 1953). Accordingly, many of the Lower Pliocene echinoids from Yule Island may be ancestral to those now living on the Great Barrier Reef and elsewhere along tropical northern Australian coasts.

This paper is the third in a series describing the echinoid fauna of the Kairuku Formation, Yule Island, Central Province, Papua New Guinea (Fig. 2). Elements of the Kairuku fauna have been described by Lindley (2001, 2003a). The present descriptions are based on collections made by the writer in January 2002, and the reader is referred to Lindley (2003a) for collection details. Specimens have been temporarily allocated Department of Geology, Australian National University repository numbers, pending their repatriation to Papua New Guinea (PNG) at the conclusion of studies, where they will be housed in the Department of Geology, University of Papua New Guinea, Port Moresby. The classification used herein follows that of Fell and Pawson (1966).

PALAEOECOLOGY

Foraminifera have been used by Haig et al. (1993: Fig. 5) to demonstrate rapid shallowing during the deposition of the Kairuku Formation, from mid-

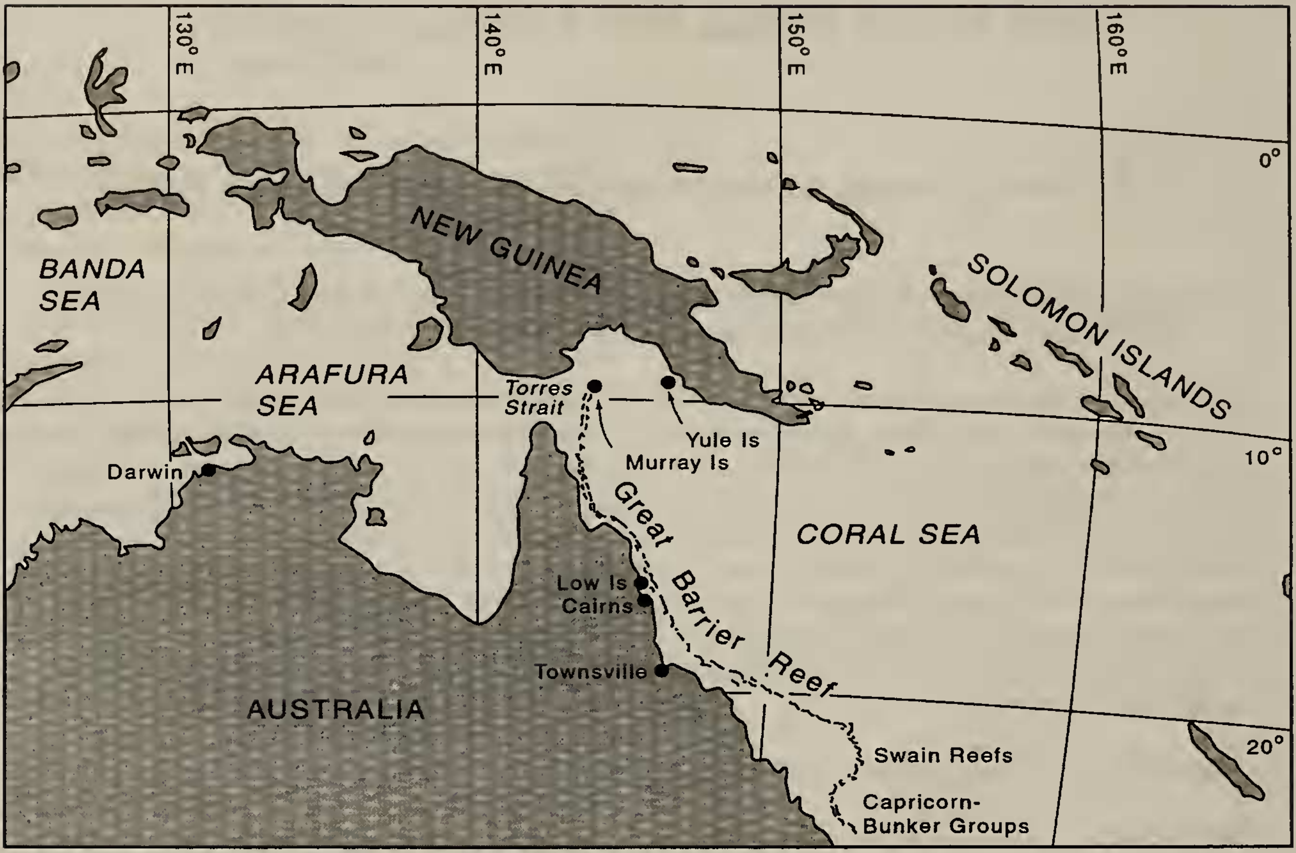

Figure 1. Locality map showing proximity of Yule Island to northern Great Barrier Reef.

neritic in the lower part to innermost neritic carbonate sand facies higher in the formation. The carbonate sand facies, predominant in the sequence collected during the present work, includes coral-rich beds and *Marginopora*-rich sands and has been interpreted by Haig et al. (1993) to have accumulated in seagrass meadows. However, Lindley (2001, 2003a) using the echinoid fauna of the Kairuku Formation, concluded that although some elements of the fauna, including the clypeasterids and laganids, were undoubtedly members of an infaunal seagrass community confined to shallow-water coarse sands, others occupied turbulent-water reef habitats and shallow-water sandy substrates constantly swept by currents. Bathymetric ranges of extant species of Yule Island echinoids indicate water depths during the deposition of the Kairuku Formation from littoral to about 40 m (Lindley 2003a), closely coinciding with Hemminga and Duarte's (2000) observation that the majority of modern seagrasses are confined to depths of less than 20 m.

Tropical echinoids are typically generalist feeders, consuming algae, seagrasses and invertebrates, and considerable data is available on the impacts of their grazing patterns on other coral reef organisms (Hatcher 1983). Echinoids are the dominant invertebrate herbivore in tropical and sub-tropical seagrass communities (McPherson 1965, 1968; Ogden et al. 1973; Hemminga and Duarte 2000). High population densities of the toxopneustid *Lytechinus* A. Agassiz, 1863 commonly leads to overgrazing events in the seagrass beds of the northern Gulf of Mexico (Valentine and Heck 1991). The toxopneustid *Tripneustes* L. Agassiz, 1841 is a dominant consumer of live seagrass leaves in PNG and Philippine seagrass beds (Nojima and Mukai 1985; Klumpp et al. 1993). Therefore, it is likely that *Cyrtechinus verruculatus* (LŸtken) and *Schizechinus* sp., close relatives of *Lytechinus* and *Tripnesutes*, were important herbivores in the seagrass meadow community at the time of deposition of the Kairuku Formation. The relative abundance of *C. verruculatus* as a fossil in the formation is probably related to the enhanced preservation potential associated with this habitat.

Turbulent, shallow-water habitats were developed in and around fringing reef, located seaward of the apparently extensive seagrass meadows. *Parasalenia poehli* Pfeffer, 1887 occupied well concealed habitats, among branches of corals or hidden in crevices beneath coral rock. The small cidaroid *Prionocidaris verticillata* (Lamarck, 1816) was restricted to the reef or lived on adjacent coral sands.

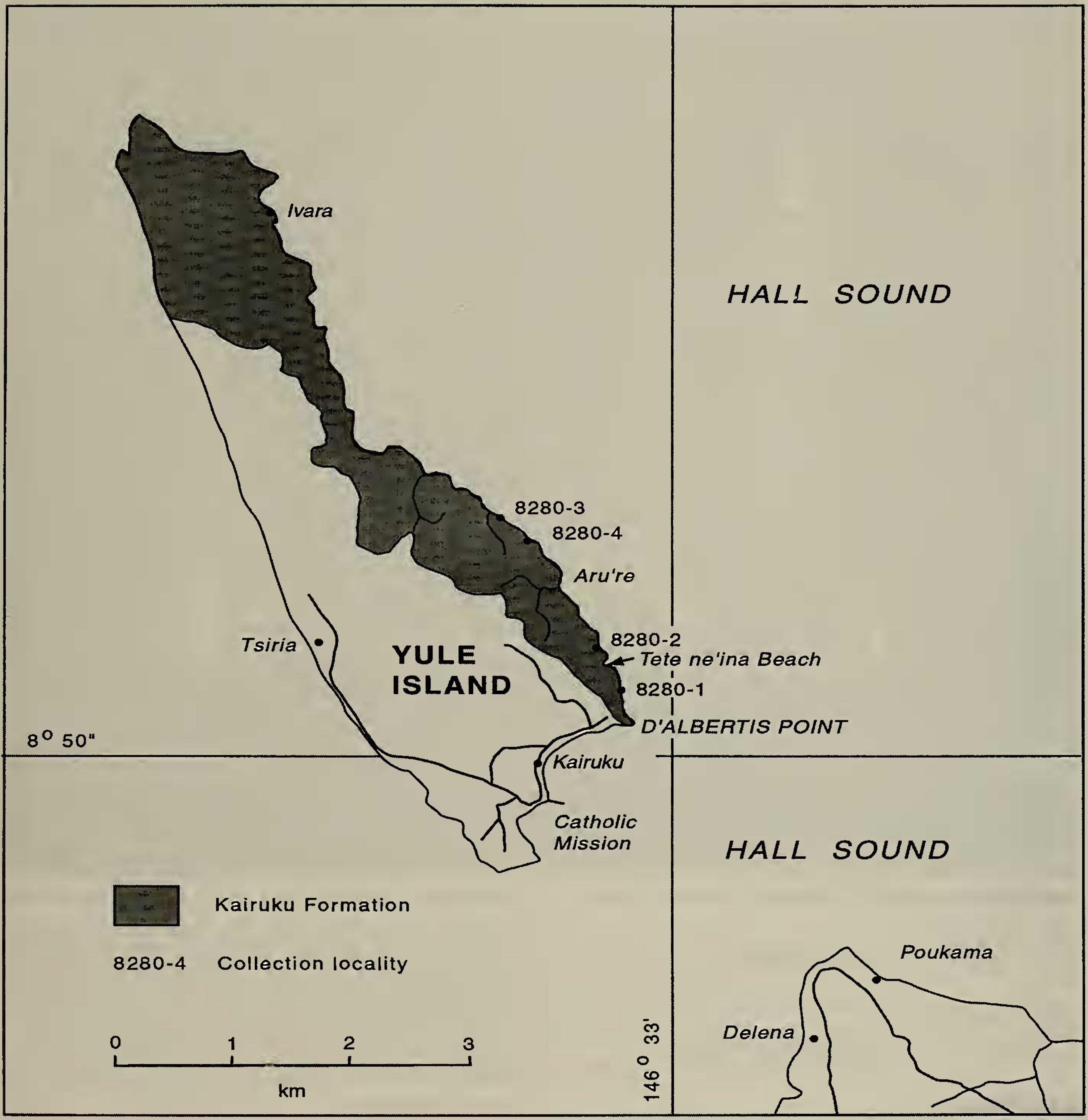

Figure 2. Yule Island, Central Province, Papua New Guinea, showing distribution of Kairuku Formation and collection localities. Base from Kairuku 1:50 000 Sheet 8280-III (Edition 1).

The large cidaroids *Phyllacanthus imperialis* var. *javana* K. Martin, 1885, and *Phyllacanthus* sp. may have favoured the outer side of the reef below low-tide mark, similar to living *P. imperialis* on the nearby Murray Islands (H.L. Clark 1946). The small temnopleuroid *Temnotrema macleayana* (Tenison-Woods) was also an element of the highly turbulent-water habitat (Lindley 2001).

Echinoids play a major role in reef destruction and may be growth limiting (Davies 1983). Glynn et al. (1979) have shown that the cidaroid *Eucidaris* Pomel, 1883, an inhabitant of intertidal reefs, grazes heavily on live corals, estimating an annual rate of bio-erosion of marine limestone attributable to this echinoid in the order of 1.7 kg/m^2. The high rate of marine erosion caused by *Eucidaris* is important in the generation of major reef-flanking sediment accumulations composed of coral and coralline particles excreted by the echinoid (Glynn et al. 1979).

The strong affinities of elements of the Yule Island fauna with both Indo-Pacific and Red Sea echinoid communities have been highlighted in Lindley (2003a) and the present work. These affinities are strongest amongst the species-rich infaunal and epifaunal echinoid communities of the seagrass meadow and the current-swept shallow-water sands. Similar geographic patterns of species richness are evident in corals and mangroves, and parallel seagrass species richness (Heck and McCoy 1979). Seagrass meadows with the richest species diversity are found in the Indo-Pacific and the Red Sea region and the parallelism present between the Yule Island echinoids and seagrasses suggests, in the words of Hemminga and Duarte (2000), that the 'constraints and processes responsible for the development and maintenance of species diversity of these taxa have been linked throughout their evolutionary history'.

SYSTEMATIC PALAEONTOLOGY

Class ECHINOIDEA Leske, 1778
Subclass PERISCHOECHINOIDEA M'Coy, 1849
Order CIDAROIDA Claus, 1880
Family CIDARIDAE Gray, 1825
Subfamily RHABDOCIDARINAE Lambert, 1900, emended Fell 1966
Genus PHYLLACANTHUS Brandt, 1835

Synonymy

Leiocidaris Desor, 1885, p. 48.

Type species

Cidarites (Phyllacanthus) dubia Brandt, 1835, p. 67, by original designation.

Remarks

Phyllacanthus Brandt, 1835 is a strictly Indo-Pacific and Australasian genus, generally restricted by most workers (Mortensen 1928; Chapman and Cudmore 1934; H.L. Clark 1946; Philip 1963; A.M. Clark and Rowe 1971) to forms having thick, smooth and cylindrical spines. It is on this basis that the Yule Island specimens can clearly be assigned to *Phyllacanthus*. Mortensen (1928) and Philip (1963) provided reviews of extant and fossil species of this genus. Seven living species have been described by Mortensen (1928, 1936), with 4 being confined to the Australian coast (Mortensen 1928; H.L. Clark 1946; Philip 1963). While fossil test fragments are rare, spines of *Phyllacanthus* are well documented in the Tertiary sequences of the Indo-Pacific region and include *Phyllacanthus javana* K. Martin, 1885 and *Phyllacanthus imperalis* var. *javana* K. Martin from the Miocene of Java (Jeannet and R. Martin 1937); *Phyllacanthus imperialis* (Lamarck) from Madagascar, Middle Pliocene of Java, Upper Miocene of Vanuatu, Lower Miocene to Pleistocene of Fiji and the Quaternary of the Suez region (Mortensen 1928; Jeannet and R. Martin 1937; Philip 1963); *Phyllacanthus dubius* Brandt, from the Middle Pliocene of Java (Jeannet and R. Martin 1937); *Phyllacanthus dubius* var. *sundaica* (R. Martin) (*non Phyllacanthus sundaica* K. Martin, 1885) from the Lower Miocene of Java (Jeannet and R. Martin 1937); and *Phyllacanthus* sp. from the Pliocene of Kenya (Philip 1963).

Phyllacanthus is a littoral genus that exhibits a marked preference for seas in which the surface temperature does not fall below the winter isotherm of 15°C (Fell 1966). Like other cidaroids it is a shallow-water dweller, with a preference for hard bottom, such as reefs (Mortensen 1928; Fell 1966). Cidaroids feed upon bottom animals, including molluscs, annelids, bryozoans, foraminifera and sponges (Fell 1966).

F. Chapman and I. Crespin (in Montgomery 1930) recorded the presence of spines of *Phyllacanthus sundaica* K. Martin, 1885 from 'the limestones of the upper part of e stage' at Delena, across Hall Sound on the mainland (= Ou Ou Limestone Member of the Middle to Late Miocene Lavao Group, Yule Island: Francis et al. 1982) (Fig. 2). This species is now considered a synonymn of *Chondrocidaris gigantea* (A. Agassiz) (Mortensen (1928: 492). The primary spines of this large species carry very coarse thorns in a random arrangement. Spines of this type were not collected from the Kairuku Formation during the present fieldwork.

Phyllacanthus imperialis var. **javana** K. Martin, 1885

Figs 3a-b

Synonymy

Phyllacanthus javana K. Martin, 1885, p. 289: Mortensen 1928, p. 503; Philip 1963, p. 202; Upper Miocene, Java.

Phyllacanthus cf. *imperialis*, cf. *dubia* Duncan and Sladen, 1885, p. 284; Miocene.

Phyllacanthus javanus: Gerth 1922, p. 517; F. Chapman and I. Crespin in Montgomery 1930, p. 57, 58; Chapman and Cudmore 1934, p. 131; Lindley 2001, p. 119; Upper Miocene, Java; Lower Pliocene, Yule Island.

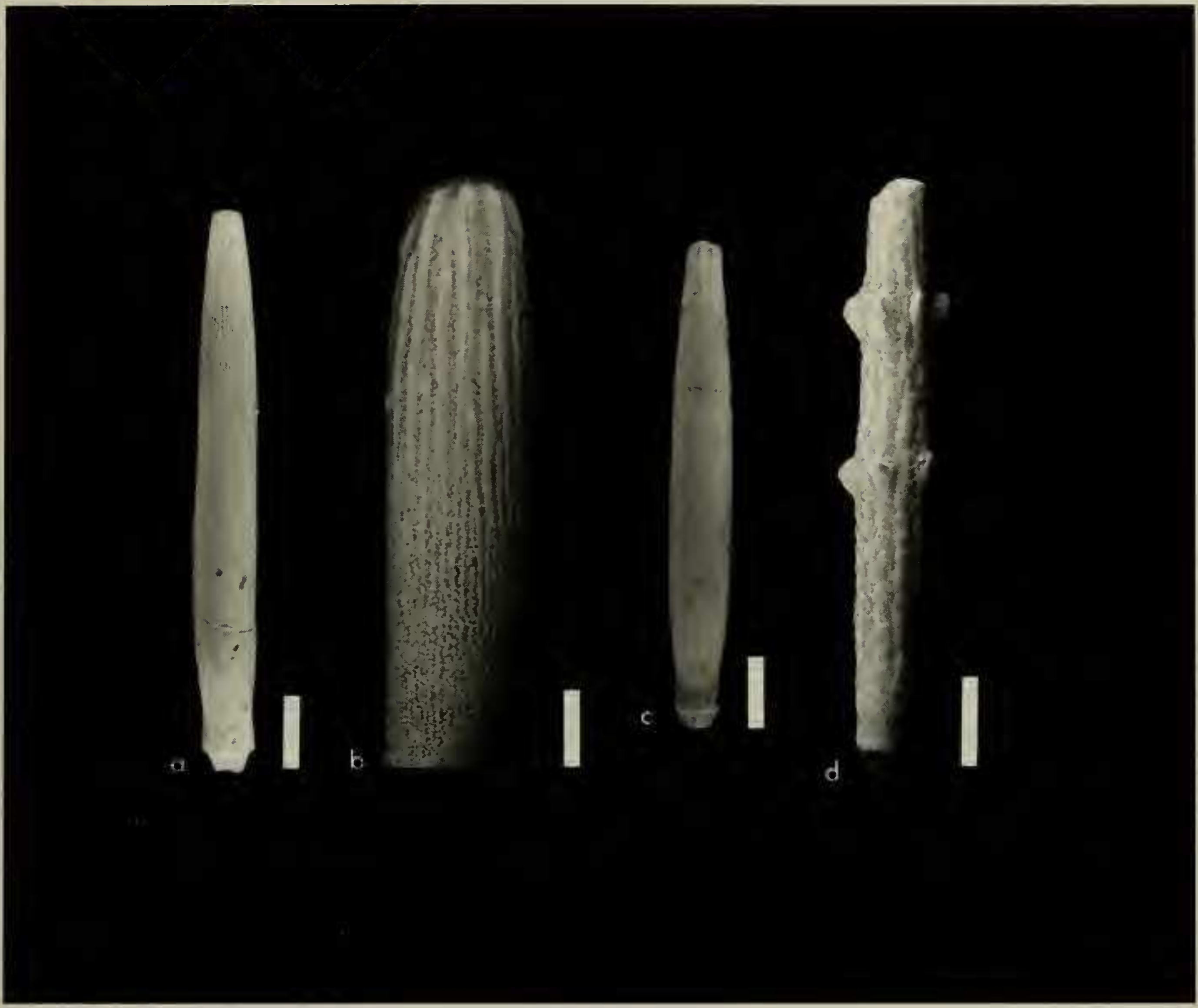

Figure 3. Cidaroid echinoids. *Phyllacanthus imperialis* var. *javana* K. Martin, 1885. Lower Pliocene, Yule Island, Central Province. 3a, ANU 60592, lateral view of spine. Bar scale = 10 mm; 3b, ANU 60598, detail of distal spine end. Bar scale = 2.5 mm. *Phyllacanthus* sp. Lower Pliocene, Yule Island, Central Province. 3c, ANU 60590, lateral view of spine. Bar scale = 10 mm. *Prionocidaris verticillata* (Lamarck). Lower Pliocene, Yule Island, Central Province. 3d, ANU 60589, lateral view of incomplete spine. Bar scale = 2.5 mm.

Leiocidaris imperialis: Jeannet 1928, p. 465.
Leiocidaris (Phyllacanthus) imperialis: Jeannet 1934, p. 13; Miocene, Java.
Phyllacanthus imperialis var. *javana* K. Martin, Jeannet and R. Martin 1937, p. 222, 223; Philip 1963, p. 202; Upper Miocene, Java.

Description

No test fragments which belong to this species have been identified. Primary spines are moderately thick, cylindrical, slightly fusiform. Spine length ranges from 36-80 mm, with a maximum diameter (measured on largest spine) of 9 mm, occurring at 1/3 distance from proximal end; spine gently tapers towards apex. Collar is finely longitudinally striated; collar length between 3.5-5 mm, with an obvious swelling at about 7 mm above collar on spine ANU 60592 of 80 mm length. Surface of shaft with a smooth appearance, but with low magnification a fine ornament is evident, consisting of low, rounded granules forming numerous (> 50) longitudinal ridges. On the distal 1/3 of spine the numerous, occasionally sinuate ridges merge, and interspaces become narrower, to form fewer (15-20), somewhat higher ridges, passing to a fluted spine end.

Remarks

Jeannet and R. Martin (1937) noted that the spines of *Phyllacanthus imperialis* var. *javana* K. Martin, 1885 from the Upper Miocene of Java, are generally slimmer and are often more pointed than those of *Phyllacanthus imperialis* (Lamarck). They also noted that the spine collar length of var. *javana*, ranging from 2.5-4 mm, is distinctly shorter than the 6 mm of *P. imperialis*. The spines of *P. imperialis*, and by association those of *P. javana*, are relatively short, usually equal to test diameter (Mortensen 1928). Mortensen (1928) considered var. *javana* a close relative to *P. imperialis*.

Phyllacanthus imperialis is the only species of *Phyllacanthus* that is widespread throughout the tropical Indo-Pacific (Mortensen 1928; H.L. Clark 1946; A.M. Clark and Rowe 1971). *Phyllacanthus imperialis* from the Murray Islands, Torres Strait, has a distinctive habitat, favouring the outer side of reef below the low-tide mark (H.L. Clark 1946).

Material

Eight isolated primary spines: ANU 60593, ANU 60596-98 from locality 8280-1; ANU 60592 from locality 8280-3; ANU 60594-95, ANU 60599 from locality 8280-4. All localities are from the east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Phyllacanthus sp.

Fig. 3c

Description

No test fragments which belong to this species have been identified. Primary spines are moderately thick, cylindrical, fusiform, with length ranging from 37.5-67.5 mm, with a maximum diameter of 9.5 mm measured at 1/3 distance from proximal end on largest spine. Spine gently tapers to apex. Collar length 3 mm in ANU 60590; details of collar ornament unknown. Surface of shaft is finely and uniformly granulated (not visible to the naked eye), the granules arranged in regular longitudinal series along length of spine. The distal 1/5 length of spine carries nine high ridges passing to a fluted spine end.

Remarks

The primary spines of *Phyllacanthus* sp. in many respects resemble those of var. *javana*, but the presence of notably fewer high ridges on the distal part of the spine is in contrast to the many ridges (15-20) present on spines of the latter form. The Yule Island spine probably represents another variety of *P. imperialis*.

Material

Two isolated primary spines: ANU 60590-91 from locality 8280-1, immediately south of Tete ne'ina Beach, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Genus PRIONOCIDARIS A. Agassiz, 1863

Synonymy

Stephanocidaris A. Agassiz, 1872 (*non* 1863).
Plococidaris Mortensen, 1909, p. 51, 51.

Type species

Cidarites pistillaris Lamarck, 1816, p. 55.

Remarks

The status of the name *Plococidaris* Mortensen, 1909, with *Cidarites bispinosa* Lamarck, 1816 designated as type species, has been the subject of discussion following Mortensen's (1928) referral of *bispinosa* to *Prionocidaris* A. Agassiz, 1863 (H.L. Clark 1946: 287; A.M. Clark and Rowe 1971: 151). These workers considered Mortensen's (1928) retention of the name *Plococidaris*, with *Cidarites verticillata* Lamarck, 1816 redesignated as type species, to be contrary to the Rules of Nomenclature, and it is regarded as a synonym of *Prionocidaris*.

Prionocidaris verticillata (Lamarck, 1816)

Fig. 3d

Synonymy

Cidarites verticillata Lamarck, 1816, p. 56.
Phyllacanthus cf. *verticillata* Duncan and Sladen, 1885, p. 284; Miocene, India.
Cidaris verticillatus: Lemoine, 1906, p. 256; Miocene, Madagascar.
Phyllacanthus verticillatus Cottreau, 1908, p. 38.
Plococidaris verticillata Mortensen, 1909, p. 51, 53; Mortensen 1928, p. 428; Jeannet and R. Martin 1937, p. 220.
Prionocidaris verticillata Döderlein, 1911, p. 242; H.L. Clark 1921, p. 145; H.L. Clark 1932, p. 211; H.L. Clark 1946, p. 287; A.M. Clark and Rowe 1971, p. 151.
Leiocidaris (Plococidaris) verticillata: Jeannet 1934, p. 11; Pliocene, Ceram.
T. Mortensen (1928), A Monograph of the Echinoidea 1, Cidaroidea, p. 428, details the previous synonymies.

Description

No test fragments which belong to this species have been identified. Primary spine small, slim, cylindrical with an incomplete length of 15 mm and a diameter of 1.5 mm. Collar length ca. 0.7 mm; details of collar ornamentation unknown. ANU 60589 with characteristic prominent whorls of blunt thorns, placed one above the other; two are preserved in specimen with three-four usually present in complete primary spines (Mortensen 1928; A.M. Clark and Rowe 1971). Smaller blunt thorns arranged in longitudinal series occur between successive whorls.

Remarks

Prionocidaris verticillata (Lamarck) is a small (30-40 mm diameter) extant species, widely distributed throughout the Indo-Pacific (Mortensen 1928; H.L. Clark 1946; A.M. Clark and Rowe 1971). In particular, the species has been recorded from the Torres Strait by H.L. Clark (1921), with a single specimen collected from Low Isles reef on the Great Barrier Reef, making it 'one of the rarest of Australian echini' (H.L. Clark 1946). In spite of the species' widespread distribution, specimens are not common (H.L. Clark 1946). The species is restricted to coral reefs and many have been found by dredging on coral sand (Mortensen 1928).

P. verticillata, with the 'very peculiar character of primary spines...may well claim to be the easiest recognizable of all species of Cidarids' (Mortensen 1928). The species, with its distinct spines, stands alone in genus *Prionocidaris* (see key of A.M. Clark and Rowe 1971), so much so that Mortensen (1928: 428) was adamant that it should represent the type of a separate genus. *Prionocidaris verticillata*, or forms closely related to the species, have been found as fossil from the Miocene of Madagascar and India, Pliocene of Ceram (Indonesia), and the Quaternary of East Africa (Mortensen 1928).

Material

One isolated primary spine ANU 60589 from locality 8280-4, northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Subclass EUECHINOIDEA Bronn, 1860
Superorder ECHINACEA Claus, 1876
Order TEMNOPLEUROIDA Mortensen, 1942

Remarks

The temnopleuroid *Temnotrema macleayana* (Tenison-Woods) is present in the Kairuku Formation on Yule Island and was redescribed by Lindley (2001).

Family TOXOPNEUSTIDAE Troschel, 1872
Genus CYRTECHINUS Mortensen, 1943

Type species

Psammechinus verruculatus Lütken, 1864, p. 98, by original designation.

Remarks

Cyrtechinus Mortensen, 1943 and the closely related *Nudechinus* H.L. Clark, 1912 and *Gymnechinus* Mortensen, 1903, are distinguished by the number of plates in the buccal membrane. Accordingly, it is very difficult or even impossible to distinguish between naked tests of species of these taxa. All are small forms found in the tropical Indo-Pacific and western Indian Ocean (A.M. Clark and Rowe 1971: 142, 143) and, as with the temnopleurids, appear to be well adapted to life in shallow-water tropical regions, especially in the case of *Nudechinus* which has developed into a considerable number of species (Mortensen 1943). All three taxa have been noted from the Torres Strait and surrounding waters (Mortensen 1943; H.L. Clark 1946; A.M. Clark and Rowe 1971). The Yule Island specimens are assigned to *Cyrtechinus* because of the striking similarity of both ambulacral and interambulacral plating diagrams with those of Hawaiian specimens of the only species, *Cyrtechinus verruculatus* (Lütken) figured by Mortensen (1943: Figs 245a-b).

Cyrtechinus verruculatus (Lütken)

Figs 4a-g, 5a-b

Synonymy

Echinus (Psammechinus) verruculatus Lütken, 1864, p. 98.

Echinus verruculatus Lütken, 1864: Sluiter 1899, p. 110.

Lytechinus verruculatus H.L. Clark, 1912: H.L. Clark 1921, p. 147; H.L. Clark 1946, p. 321.

Cyrtechinus verruculatus (Lütken): Mortensen 1943, p. 393; A.H. Clark 1952, p. 267; A.M. Clark and Rowe 1971, p. 142, 143.

Cyrtacanthus verruculatus (Lütken): A.M. Clark and Rowe 1971, p. 156.

Stomechinid (?), Lindley 2001, p. 126.

T. Mortensen (1943), A Monograph of the Echinoidea 3(2), Camarodonta 1, p. 393, and A.M. Clark and F.W.E. Rowe (1971), Monograph of Shallow-Water Indo-West Pacific Echinoderms, p. 142, 143, details the previous synonymies.

Description

Test small, very regularly hemispherical; distinctly subpentagonal circumference in the largest specimens. Ambitus relatively low; distinctly sunken towards the peristome. It appears not to exceed a size

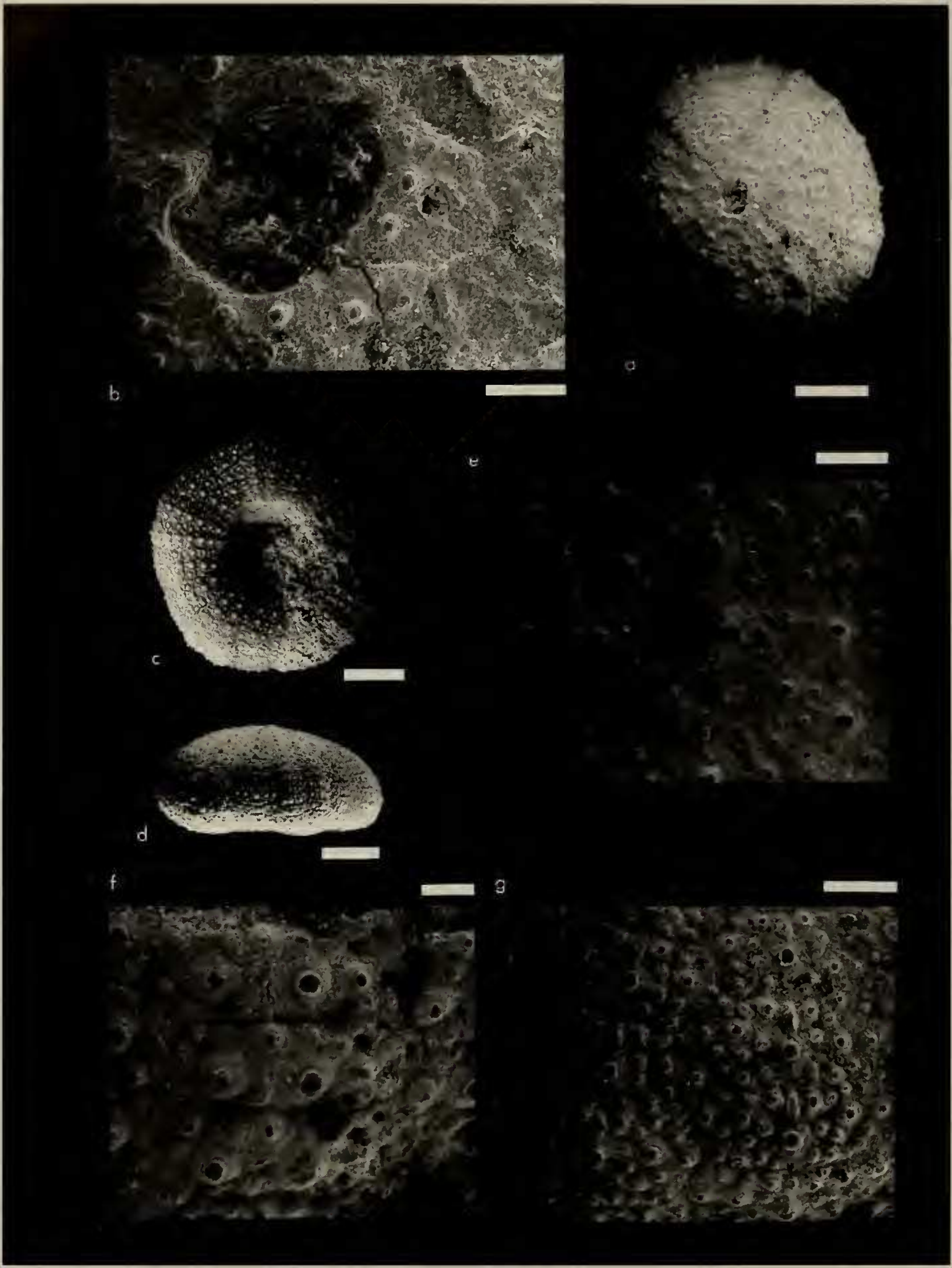

Figure 4. *Cyrtechinus verruculatus* **(Lütken). Lower Pliocene, Yule Island, Central Province. 4a-b, ANU 60576, aboral view. Bar scale = 2.5 mm; portion of apical disc, showing periproct and small tubercles adapical to genital pores. Bar scale = 0.5 mm. 4c-f, UPNG F1184, oral, lateral views. Bar scale = 5 mm; apical disc with madreporite top centre, posterior to lower right. Bar scale = 1 mm; ambulacral plating at ambitus (refer to Fig. 5b for plating diagram). Bar scale = 0.5 mm. 4g, ANU 60572, interambulacral plating at ambitus (refer to Fig. 5a for plating diagram). Bar scale = 1 mm.**

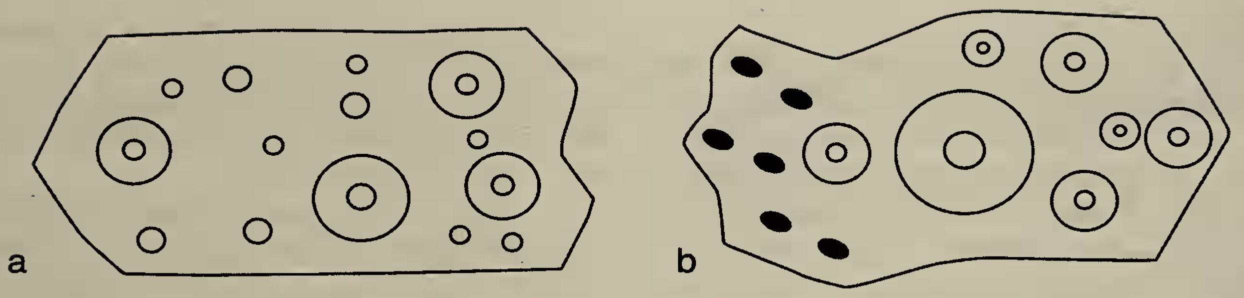

Figure 5. ***Cyrtechinus verruculatus*** **(Lütken). Lower Pliocene, Yule Island, Central Province. 5a-b, plating diagrams at ambitus for interambulacrum, ambulacrum.**

of c. 24 mm horizontal diameter (Table 1). Dimensions are comparable with those presented by Mortensen (1943) for the species, ranging from 10.5 to 24 mm horizontal diameter, with a single specimen of 27 mm considered by him to be very old. Both ambulacra and interambulacra densely covered with tubercles.

Apical system small with a central periproct. In smaller specimens (ANU 60576) Ocular I is insert; in larger specimens (UPNG F1184) both Oculars I and V are narrowly insert. The same relationships were described by Mortensen (1943) in Recent specimens of the species from the central Pacific and East African coast. Tubercles on apical plates increase in size with age, with older specimens having a single large tubercle located adapically to genital pore; young specimens (ANU 60576) have three small, equi-sized tubercles adapical to the genital pore.

Ambulacra at ambitus are about 2/3 width of interambulacra. Ambulacral plates compound, trigeminate, pore pairs in arcs of three. A prominent elevated primary tubercle is present in the middle of each plate, forming a vertical series. Tubercles imperforate, noncrenulate, as large as interambulacral primaries. Large secondary tubercles present admesially to the primary ambulacral tubercles, but do not form prominent vertical series. The number and arrangement of tubercles generally remains the same in various sized specimens. Interambulacral plates are about equal in height to opposite ambulacral plate. Each possesses a sub-central prominent imperforate, noncrenulate primary tubercle; each primary tubercle is surrounded by a semi-circular series of variously sized secondaries. In larger specimens (ANU 60572) there is a tendency for the development of weak ridging radiating from the primary tubercle towards secondaries, forming a sculpturing reminiscent of the temnopleurids.

Peristome large, about 1/3-1/2 horizontal diameter of test; twice size of apical system in larger specimens (Table 1). Gill slits are distinct and small. Tubercles of the oral surface, particularly surrounding the peristome, with a distinctly enlarged, elevated boss compared with those of the apical surface.

TABLE 1. ***Cyrtechinus verruculatus*** **(Lütken): Test dimensions in millimetres.**

Specimen	Diameter	Height	Apical system	Peristome
F1184	24	9	5	10
60578	21.5	7	-	9
60579	21	-	-	-
60577	19	9	4	-
60572	19	8	4	-
60582	18.5	9	-	7
60580	18	6	4	-
60583	17	-	-	-
60581	16.5	-	-	6
60576	16	7	4	6.5
60573	14.5	6	2.5	-
60575	14	6	-	-
60574	11	6	2.5	-

Remarks

Cyrtechinus verruculatus (Lütken) is a Recent species from the tropical Indo-West Pacific (Mortensen 1943; A.M. Clark and Rowe 1971). In particular, it has been recorded from the Java Sea, Sulu Sea and Torres Strait (Mortensen 1943). The fossil record of *C. verruculatus* is problematic given the uncertainty in distinguishing naked tests from those of the closely allied *Nudechinus* H.L. Clark, 1912, and *Gymnechinus* Mortensen, 1903 (Mortensen 1943: 398, 399; A.M. Clark and Rowe 1971). Fossil specimens from the Pleistocene deposits of Egypt have been referred to *Nudechinus scotiopremnus* H. L. Clark, 1912, a species common in the Red Sea (Mortensen 1943). Specimens possibly referrable to *C. verruculatus* have been described from the East African coast, from the Pliocene of Mombasa Island and from Mozambique (Mortensen 1943). However, it is suffice to say that forms identical with *C. verruculatus* or an ancestor of the species were present in the western Indian Ocean during the Plio-Pleistocene.

Cyrtechinus is a small form typically restricted to the littoral zone. The low hemispherical test with a low down ambitus, was interpreted by Lindley (2001) as an adaptive strategy, giving stability in currents on either rocky or sandy substrates. Closely allied forms such as *Lytechinus* and *Tripneustes* are dominant consumers of live seagrass leaves in tropical seagrass communities (Nojima and Mukai 1985; Klumpp et al. 1993). *Cyrtechinus verruculatus* is interpreted as a seagrass grazer in meadows constantly swept by currents.

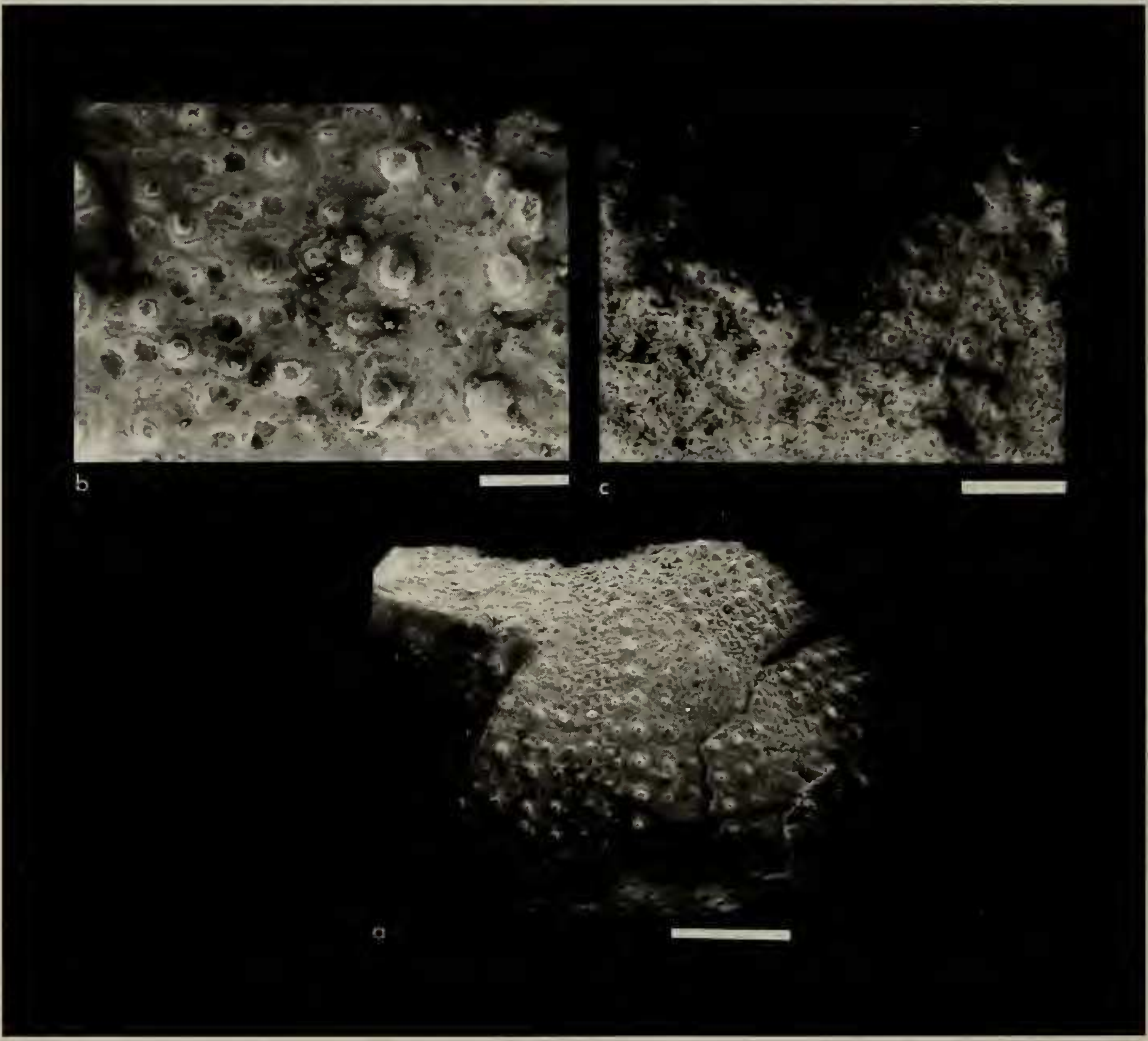

Figure 6. *Schizechinus* cf. *tuberculatus* (Pomel). Lower Pliocene, Yule Island, Central Province. 6a-c, ANU 60600, lateral view with peristome to top. Bar scale = 5 mm; ambulacral plating at ambitus (refer to Fig. 7a for plating diagram). Bar scale = 1 mm; portion of peristome showing deep gill slits. Bar scale = 2 mm.

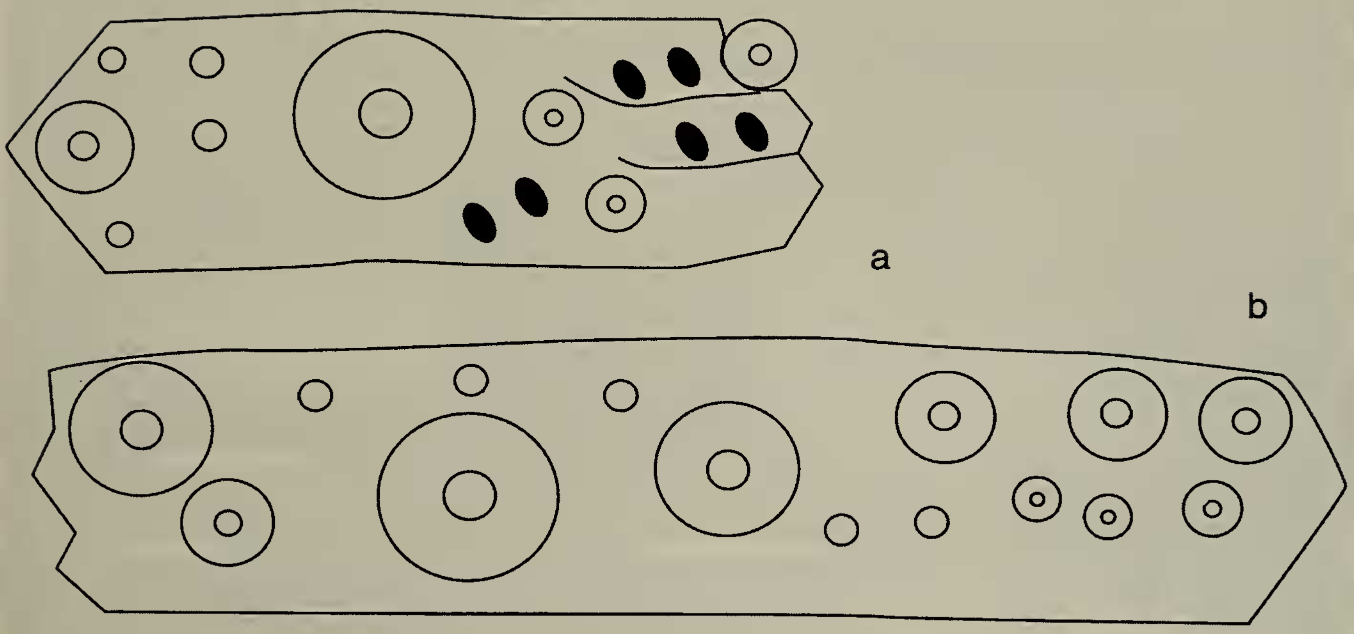

Figure 7. *Schizechinus* cf. *tuberculatus* (Pomel). Lower Pliocene, Yule Island, Central Province. 7a-b, plating diagrams at ambitus for ambulacrum, interambulacrum.

Material

Fourteen complete tests: ANU 60572-73, ANU 60575-83 from locality 8280-3; ANU 60574, ANU 60587 from locality 8280-4; and UPNG F1184 collected by R. Perembo from locality 24 of Francis et al. (1982) = locality 8280-3. All localities are northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Genus SCHIZECHINUS Pomel, 1869

Synonymy

Toxophyma Lambert and Thiéry, 1925, p. 280.

Type species

Anapesus tuberculatus Pomel, 1887, p. 298, by original designation.

Remarks

The referral of the Yule Island form to *Echinus* cf. *stracheyi* by F. Chapman and I. Crepsin (in Montgomery 1930) is doubtful. The presence of a primary tubercle on every ambulacral plate clearly distinguishes the Yule Island species from the echinid *Echinus* Linné, 1758, in which primaries are present only on every alternate (or every third) ambulacral plate (Fell and Pawson 1966).

The Yule Island species can be confidently assigned to *Schizechinus* Pomel, 1869 using Mortensen's (1943) key for the Family Toxopneustidae. *Schizechinus* is the only large toxopneustid with trigeminate ambulacral plates each bearing primary and secondary tubercles arranged in regular parallel series (Mortensen 1943; Fell and Pawson 1966). *Lytechinus* A. Agassiz, 1863 is another toxopneustid with a similar test, but differs from *Schizechinus* in that the secondary tubercles do not form a regular series. Mortensen (1943) regards *Schizechinus* a near relation of *Lytechinus*. *Schizechinus* is known only from fossils, from the Mio-Pliocene of North Africa (Malta and Algeria) and Europe.

Schizechinus cf. **tuberculatus** (Pomel)

Figs 6a-c, 7a-b

Synonymy

Schizechinus tuberculatus Pomel, 1869, p. XLII.

Echinus cf. *stracheyi*: F. Chapman and I. Crespin in Montgomery 1930, p. 57; Lower Pliocene, Yule Island.

Description

No complete test is available. However, the portion of test preserved in ANU 60600 suggests a large test, c. 60 mm diameter, comparable with forms figured by Mortensen (1943). Test apparently of high hemispherical shape, inferred from shape of ambital region preserved in ANU 60601. Ambital outline inferred to be circular, relatively low; oral surface

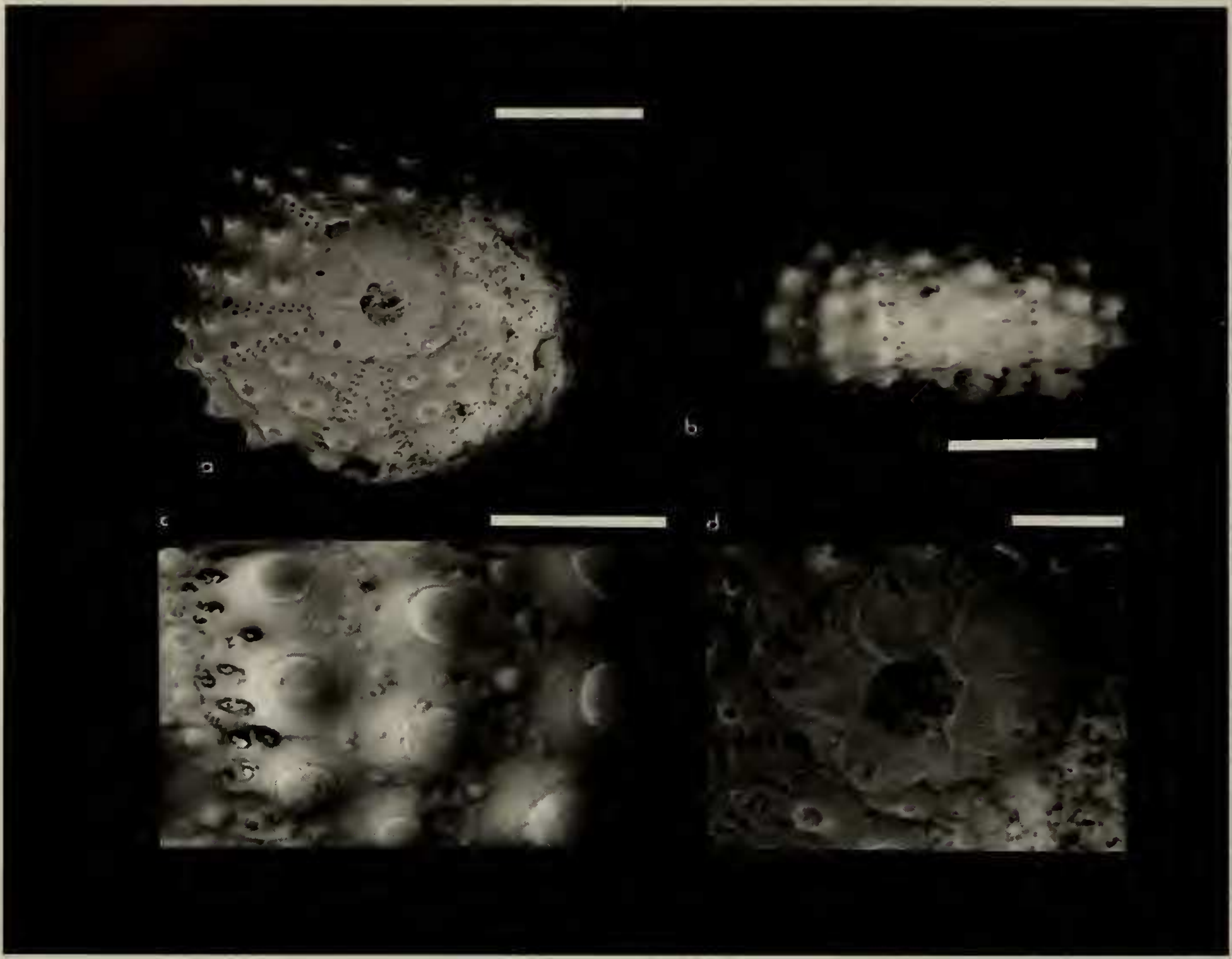

Figure 8. ***Parasalenia poehli*** **Pfeffer, 1887. Lower Pliocene, Yule Island, Central Province. 8a-d, ANU 60584, aboral, lateral views. Bar scale = 5 mm; ambulacral plating at ambitus (refer to Fig. 9a for plating diagram). Bar scale = 2 mm; apical disc, with posterior to lower left. Bar scale = 2 mm.**

flattened and distinctly sunken towards peristome (ANU 60600). Details of apical system unknown. Ambulacra at ambitus are about 1/2 width of interambulacra. Ambulacral plates compound, trigeminate pore pairs in arcs of three. A prominent elevated imperforate, noncrenulate primary tubercle, about the same size as interambulacral ones, is present in the middle of each plate, forming a vertical series. Large secondary tubercles are also present on each plate, forming a regular perradial series parallel with the primary series. A varying number of randomly placed small tubercles cover the plates.

Interambulacral plates at ambitus are about equal in height and twice the width of opposite ambulacral plate. Each possesses a sub-central imperforate, noncrenulate primary tubercle, forming a regular vertical series. Each primary is flanked by two secondaries, also forming regular series parallel with the primary series. Varying numbers of randomly placed small tubercles cover the remainder to each plate.

Peristome sunken, c. 10 mm diameter in ANU 60600; gill slits are distinct, deep.

Remarks

This large regular echinoid is represented only by fragmentary material, indicative of the poor preservation potential of such fragile forms (Kier 1977). However, the Yule Island material is tentatively referred to *Schizechinus tuberculatus* (Pomel), figured by Mortensen (1943: Fig. 291a,b) and Fell and Pawson (1966: Fig. 320, 3b,c), on the basis of similarity of (a) ambulacral and interambulacral plating in the ambital region, and (b) inferred test shape. *Schizechinus tuberculatus* (Pomel) is a Miocene echinoid from Algeria. The Yule Island occurrence is the first record of the subtropical *Schizechinus* in the southern hemisphere.

Schizechinus also includes another 12 species, predominantly from the Miocene and Pliocene of the

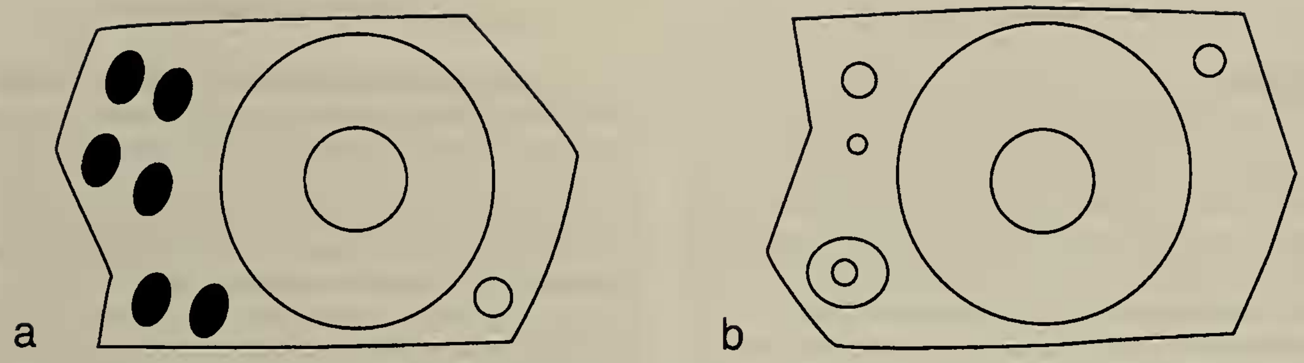

Figure 9. *Parasalenia poehli* Pfeffer, 1887. Lower Pliocene, Yule Island, Central Province. 9a-b, plating diagrams at ambitus for ambulacrum, interambulacrum.

Mediterranean region and Europe (Mortensen 1943). Mortensen (1943) figured two of these species, viz: *Schizechinus angulosus* (Pomel) from the Miocene of Algeria and *Schizechinus duciei* (Wright) from the Miocene of Malta. Test shape is an obvious difference between figured species. Little information on the remaining ten species is presently available to the writer and the Yule Island form may well represent a new species.

Material

Three fragmentary tests: ANU 60600 is a preserved portion of the oral surface, with the margin of the peristome and gill slits; ANU 60601 is a portion of an interambulacrum at the ambitus, with some of the oral surface; ANU 60602 is a portion of the ambital surface. ANU 60600-01 were collected from locality 8280-1; ANU 60602 from locality 8280-3. All localities are from the east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

Order ECHINOIDA Claus, 1876
Family PARASALENIIDAE Mortensen, 1903
Genus PARASALENIA A. Agassiz, 1863

Synonymy

Cladosalenia A. Agassiz, 1872, p. 148.

Type species

Parasalenia gratiosa A. Agassiz, 1863, p. 22.

Parasalenia poehli Pfeffer, 1887

Figs 8a-d, 9a-b

Synonymy

Parasalenia pöhlii Pfeffer, 1887, p. 110: H.L. Clark, 1912, p. 369; Lambert and Thiéry, 1914, p. 269; H.L. Clark, 1922, p. 142; H.L. Clark, 1925; H.L. Clark, 1928, p. 469; Mortensen, 1940, p. 49; Mortensen, 1943, p. 272; H.L. Clark, 1946, p. 331.

Parasalenia gratiosa de Meijere, 1904, p. 98.

Parasalenia poehli: A.M. Clark and Spencer Davies, 1966, p. 599, 603; A.M. Clark and Rowe, 1971, p. 142, 157.

Description

Test small, distinctly elongate and low, ANU 60585 measuring 8 x 7.5 x 4.5 mm and ANU 60584 20 x 18 x 9 mm. Dimensions are comparable with those of Mortensen (1943), who noted a range in test length x height from 8 x 3 mm to 17 x 6 mm, and H.L. Clark (1928, 1946), who noted a single specimen from the northern Great Barrier Reef 16 x 13 x 7 mm. Details of oral surface unknown. Mortensen (1943) noted that the test is not very strong, and is easily broken.

Apical system is dicyclic, 8 mm x 6.5 mm, elongate in the plane of long axis of test. Diameter of periproct is about 1/4 of the long diameter of the apical system. The madreporite is limited in size, with pores only occupying about 1/3 of plate. Genital plates are smooth and are without tubercles. Oculars are widely exsert and small.

Ambulacra at ambitus match the width of interambulacra. Ambulacral plates compound, trigeminate, pore pairs in arcs of three. Pore zones very narrow. A large primary tubercle occupies much of plate, leaving little space for development of secondary tubercles and granules. Primary tubercles are imperforate and non-crenulate; the mamelon is relatively large and areole indistinct. Secondary tubercles and granules are either absent or number at most one or two per plate. Primary tubercles on the 2-3 uppermost ambulacral plates are very much diminished in size. Interambulacral plates are about equal in height to opposite ambulacral plate. Primary interambulacral tubercles very large, leaving only a restricted adradial space for 2-3 secondary tubercles. Secondary tubercles do not form regular horizontal or vertical series.

Details of peristome unknown.

Remarks

Parasalenia A. Agassiz, 1863 includes two Recent species, *Parasalenia gratiosa* A. Agassiz, 1863 and *Parasalenia poehli* Pfeffer, 1887, with an Indo-Pacific and Red Sea distribution, and a single fossil species, *Parasalenia fontannesi* Cotteau, 1913, from the Lower Miocene of France (Mortensen 1943; Fell and Pawson 1966). H.L. Clark (1928, 1946) noted a single specimen of *P. poehli* from the northern Great Barrier Reef, representing the only documented occurrence of the species in Australian waters.

There has been considerable discussion regarding the validity of *poehli* as a species (Mortensen 1943; H.L. Clark 1946). *Parasalenia poehli* is a much smaller form, with the largest recorded being 17 mm long, half that of *gratiosa* (Mortensen 1943). Both Mortensen (1943) and H.L. Clark (1946) agree that periproct size is important in distinguishing the two forms. The periproct of *poehli* is relatively smaller, about 1/4 of the long diameter of the apical system; this compares with 1/3-1/2 that length in *gratiosa*. H.L. Clark (1946) regarded the presence or absence of tubercles on genital plates as an important diagnostic character, but Mortensen (1943) believed this character to be 'quite unreliable'. Both Mortensen (1943) and H.L. Clark (1946) observed that the genital plates of *gratiosa* carry tubercles, but not in *poehli*. In addition to periproct size, Mortensen (1943) emphasised the size of primary tubercles, with *poehli* having smaller primary tubercles, with more space for secondary tubercles, than *gratiosa*. A.M. Clark and Rowe (1971) recognised both *poehli* and *gratiosa* as valid species, but using differing characters to those of Mortensen (1943) and H.L. Clark (1946). They distinguished species using, amongst other characters, the length of primary spines relative to test length. In the case of *gratiosa* spines are about equal to test length, whereas for *poehli*, primary spines are only about half as long as test length. Spine length in the parasaleniids is expected to be proportionate to primary tubercle size, and this latter character, as used by Mortensen (1943), is therefore clearly useful in distinguishing naked tests.

Parasalenia occupies generally well concealed habitats, among the branches of corals or hidden in crevices and cavities beneath coral rock (H.L. Clark 1946). Mortensen (1943) noted a bathymetric range extending from littoral to c. 70 m.

Material

Two tests: ANU 60584 from locality 8280-3; ANU 60585 from locality 8280-4. Both localities are northwest of Aru're village, east coast of Yule Island, Central Province, PNG. Kairuku Formation, Lower Pliocene.

ACKNOWLEDGMENTS

The specimens described in this paper were collected by the writer during fieldwork on Yule Island in January 2002. For the efficient execution of this fieldwork, the writer gratefully acknowledges the assistance and hospitality of Sr. Elizabeth of the Bishop's Office, Diocese of Bereina, Port Moresby and the OLSH Sisters at the Yule Island Mission. Alphonese Aisi and Ben and Nahau Roama of Yule Island, with Daniel Salamas of Port Moresby, all helped during fieldwork. Photography of specimens was completed by Dr. Roger Heady of the Scanning Electron Microscopy Unit, ANU, and Dr. R.E. Barwick. Parts of the manuscript were read by Prof. K.S.W. Campbell. Dr. Ulrike Troitzsch is kindly acknowledged for her translation from German of parts of Jeannet and R. Martin (1937). This work was completed while the writer was a Visiting Fellow in the Department of Geology, ANU, and Dr. Patrick De Deckker, Head of Department, is thanked for the provision of departmental facilities.

REFERENCES

[Additional to those listed in Lindley (2002)]

Australasian Petroleum Company Proprietary. (1961). Geological Results of Petroleum Exploration in Western Papua 1937-1961. *Journal of the Geological Society of Australia* **8(1)**, 1-133.

Chapman, F. and Cudmore, F.A. (1934). The Cainozoic Cidaridae of Australia. *Memoirs of the National Museum Melbourne* **8**, 126-149.

Clark, A.H. (1911). The comparative age of the Recent crinoid faunas. *American Journal of Science*, Series **4**, Volume **32**, 127-132.

Clark, A.H. (1952). Echinoderms from the Marshall Islands. *Proceedings of the U.S. National Museum* **102**, 265-303.

Clark, A.M. (1975). The Swain Reefs Expedition: Crinoidea. *Records of the Australian Museum* **29**, 391-406.

Clark, H.L. (1921). The echinoderm fauna of Torres Strait. *Carnegie Institution of Washington*, Publication **214**, Department of Marine Biology, Volume **10**, 1-224.

Clark, H.L. (1928). The sea-lilies, sea-stars, brittle stars and sea-urchins of the South Australian Museum. *Records of the South Australian Museum* **3(4)**, 361-482.

Clark, H.L. (1932). Echinodermata (other than Asteroidea). *Scientific Reports of the Great Barrier Reef Expedition* **4**, 197-239.

Davies, P.J. (1983). Reef growth. In 'Perspectives on Coral Reefs' (Ed. D.J. Barnes) pp. 69-106. (Australian Institute of Marine Science Contribution Number 200: Townsville).

Ekman, S. (1953). 'Zoogeography of the Sea'. (Sidgwick and Jackson Limited: London).

Endean, R. (1953). Queensland faunistic records - 3. Echinodermata (excluding Crinoidea). *Papers of Department of Zoology, University of Queensland*

Department of Zoology, University of Queensland **1**, 53-60.

Endean, R. (1956). Queensland faunistic records - 4. Further records of Echinodermata (excluding Crinoidea). *Papers of Department of Zoology, University of Queensland* **1**, 123-140.

Endean, R. (1957). The biogeography of Queensland's shallow-water echinoderm fauna (excluding Crinoidea), with a rearrangement of the faunistic provinces of tropical Australia. *Australian Journal of Marine and Freshwater Research* **8**, 233-273.

Fell, H.B. (1966). Cidaroids. In 'Treatise on Invertebrate Paleontology, Part U, Echinodermata 3' (Ed. R.C. Moore) pp. U312-U340. (Geological Society of America and University of Kansas Press: Lawrence).

Fell, H.B. and Pawson, D.L. (1966). Echinacea. In 'Treatise on Invertebrate Paleontology, Part U, Echinodermata 3' (Ed. R.C. Moore) pp. U367-U440. (Geological Society of America and University of Kansas Press: Lawrence).

Gibbs, P.E., Clark, A.M. and Clark, C.M. (1976). Echinoderms from the northern region of the Great Barrier Reef, Australia. *Bulletin of the British Museum Natural History* (Zoology) **30(4)**, 103-144.

Glynn, P.W., Wellington, G.M. and Birkeland, C. (1979). Coral reef growth in the Galapagos: Limitation by sea urchins. *Science* **203**, 47-49.

Hatcher, B.G. (1983). Grazing in coral reef ecosystems. In 'Perspectives on Coral Reefs' (Ed. D.J. Barnes) pp. 164-179. (Australian Institute of Marine Science Contribution Number 200: Townsville).

Heck, K.L. and McCoy, E.D. (1979). Biogeography of seagrasses: evidence from associated organisms. *New Zealand Department of Scientific and Industrial Research Information Series*, **137**, 109-128.

Kier, P.M. (1977). The poor fossil record of the regular echinoid. *Palaeobiology* **3**, 168-174.

Klumpp, D.W., Salita-Espinosa, J.T. and Fortes, M.D. (1993). Feeding ecology and trophic role of sea urchins in a tropical seagrass community. *Aquatic Botany*, **45**, 205-229.

Lindley, I.D. (2003a). Echinoids of the Kairuku Formation (Lower Pliocene), Yule Island, Papua New Guinea: Clypeasteroida. *Proceedings of the Linnean Society of New South Wales* **124**, 29-40.

McPherson, B.F. (1965). Contributions to the biology of the sea urchin *Tripneustes ventricosus*. *Bulletin of Marine Science* **15**, 228-244.

McPherson, B.F. (1968). Contributions to the biology of the urchin *Eucidaris tribuloides* (Lamarck). *Bulletin of Marine Science* **18**, 400-433.

Mortensen, T. (1928). A Monograph of the Echinoidea 1, Cidaroidea. C.A. Reitzel, Copenhagen. 551p.

Mortensen, T. (1936). *Phyllacanthus forcipulatus*, sp. nov., a new cidarid from the Indian Ocean. *Records of the Indian Museum, Calcutta* **38**, 307-309.

Mortensen, T. (1943). A Monograph of the Echinoidea 3(2), Camarodonta 1. C.A. Reitzel, Copenhagen. 553p.

Nojima, S. and Mukai, H. (1985). A preliminary report on the distribution pattern, daily activity and movement pattern of a seagrass grazer, *Tripneustes gratilla* (Echinodermata: Echinoidea), in a Papua New Guinean seagrass bed. *Special Publication of Mukaishishima Marine Biology Station*, 173-183.

Ogden, J.C., Abbott, D.P. and Abbott, I.A. (1973). Studies on the activity and food of the echinoid *Diadema antillarum* Philippi on a West Indian patch reef. *West Indies Laboratory Special Publication* **2**, 1-96.

Philip, G.M. (1963). The Tertiary echinoids of southeastern Australia. 1 Introduction and Cidaridae (1). *Proceedings of the Royal Society of Victoria* **76**, 181-226.

Struckmeyer, H.I.M., Yeung, M. and Pigram, C.J. (1993). Mesozoic to Cainozoic plate tectonics and palaeogeographic evolution of the New Guinea region. In 'Petroleum Exploration and Development in Papua New Guinea: Proceedings of the Second PNG Petroleum Convention, Port Moresby' (Eds. G.J. Carman and Z. Carman) pp. 262-290. (PNG Chamber of Mines and Petroleum: Port Moresby).

Valentine, J.F. and Heck, K.L. (1991). The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* **154**, 215-230.